DEVELOPMENT OF THE SEA ANEMONE, HALIPLANELLA LUCIAE. V. LONGITUDINAL FISSION AND THE ORIGIN OF MONO-, DIAND TRI-GLYPHIC INDIVIDUALS.

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DEVELOPMENT OF THE SEA ANEMONE, *HALIPLANELLA LUCIAE*. V. LONGITUDINAL FISSION AND THE ORIGIN OF MONO-, DI- AND TRI-GLYPHIC INDIVIDUALS.[1)]

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The present species were classified into four races by UCHIDA (1936), viz., orange-striped, orange-yellow-striped, yellow-striped and non-striped. Many studies have been done concerning to asexual reproduction of the orange-striped race and closely related species (ATODA, 1954a, 1972; TORREY and MERY, 1904; HARGITT, 1914; DAVIS, 1919; MIYAWAKI, 1952). In the remaining three races, however, the studies on this subject and the correlation between these four races have almost not been published to date.

On the other hand, the orange-striped race executed pedal laceration and originated mono-, di- and tri-glyphic regenerates and rarely tetraglyphic ones (ATODA, 1972). Though the correlation between forms of laceration pieces and such regenerates has been reported in the previous paper (ATODA, 1960), still many problems have been remained.

MATERIAL AND METHOD

Both the orange-striped race and the non-striped one were collected from Shôbuta and various seashores and islands of Matsushima Bay, Miyagi Prefecture. The individuals belonging to the former always exceedingly outnumbered than those of the latter. The remaining two races, however, were rarely found in these localities. On the contrary, in addition to the orange-striped race, a considerable number of individuals belonging to the other races were collected from Tashiro Island and the three races except the yellow-striped one were found in Mahanashi Island. The yellow-striped race, however, was collected from Yunoshima in the vicinity of Asamushi Marine Biological Station, Aomori Prefecture, where a great number of this individuals were aggregated (August, 1965).

All of the following observations and experiments were made by the same methods as those described in my previous papers (ATODA, 1960, 1973), and

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regenerates developed from laceration pieces were kept in a thermostat at about 25°C for several months.

Observations

A. Longitudinal fission

1. Orange-striped race (OS) (Fig. 1, A, Plate VII, Fig. 1)

a. Process of fission (Plate VII, Figs. 5–11)

Many anemones collected from Tashiro Island acted frequent laceration, while only nine individuals executed fission.

The anemone stuck fast to some substratum with its pedal disc and did not change its body length throughout all processes of fission. In the beginning of fission the body became conspicuously flattened and elongated towards direction along the longitudinal axis of the oral aperture, and the oral disc nearly came in touch with the pedal disc. It seemed that the body was pulled forcibly towards its either side along mentioned axis, and in consequence the pedal disc begun to tear, resulting some large rent in about middle of the disc. The rent gradually became larger and both the pedal disc and oral one finally split. Then the edge of the wound was somewhat rolled inside and a strong tension loaded on the body seemed to decrease. As a result it took a fairly long time to be completely divided the body into halves. The wound was soon closed by fusion of its edge and the fused part remained as a whitish streak, where became gradually widened. Since then several number of new mesenteries and orange stripes appeared in this regenerative part. At first 5 to 7 light yellow stripes appeared on every one new mesneteric chambers, then changed reddish yellow and finally deep orange in colour.

b. Regenerates

Twenty regenerates in about four to eight months after fission comprised 4 mono-, 14 di - and 2 tri-glyphic individuals. They belonged to 13 types, of which 8 were the same ones as those found in the individuals produced by laceration and collected from the fields (Atoda, 1972) and the remaining five, OS.1–OS.5 (Fig. 2) were peculiar ones (Table 1).

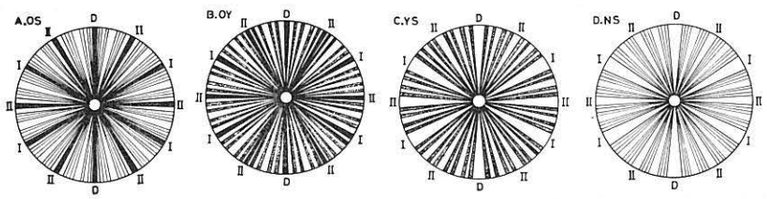


Fig. 1. Diagrammatic figures of the orange- (A. OS), orange-yellow- (B. OY), yellow- (C. YS) and non-striped (D. NS) races. D, directive chamber; I and II, the first and second orders of chambers.

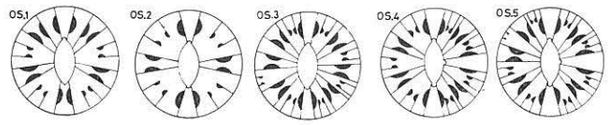


Fig. 2. Diagrammatic figures of peculiar types produced by fission in the orange-striped race. OS. 1, mono-; OS. 2 and OS. 3, di-; OS. 4 and OS. 5, tri-glyphics.

Table 1
Types of 20 regenerates in the orange-striped race.

	Monoglyphics				Diglyphics							Triglyphics	
Types	III	X	OS. 1	XXX	OS. 2	D	N	V	I	OS. 3	W	OS. 4	OS. 5
No. of regenerates	1	1	1	1	2	1	6	2	1	1	1	1	1
%	5.0	5.0	5.0	5.0	10.0	5.0	30.0	10.0	5.0	5.0	5.0	5.0	5.0

2. Orange-yellow-striped race (OY) (Plate VII, Fig. 2)

The anemones belonging to this race had orange stripes on the same order of mesenteric chambers as those of the orange-striped race, and in addition to them, four yellow stripes were found between two orange ones (Fig. 1, B). In the number of two kinds of stripes, however, there were wide variations (Table 2).

Twenty-four anemones executed frequent fission at 20–23°C of sea water temperature, and in 14 anemones their bodies were divided into two equal or unequal poritions by fission and in 5 anemones, into three unequal portions and in one anemone, into four unequal ones.

The fissiparous process was closely similar to that found in the orange-striped race (Plate VII, Figs. 12–15), and in most anemones their bodies became torn at some mesenteric chambers with orange stripes. Fission resulting three regnerates from a single parent was observed in the individual with a triangular form (Plate VII, Figs. 16–19). The pedal disc, then the oral aperture became torn and a large rent appeared at the center of the oral disc. Then the body split in three portions with respective vertexes of triangles, and perhaps only two portions had siphonoglyphs respectively.

In two to three months after fission several number of two kinds of stripes appeared at about same time in regenerative part, and the forms of 43 well-developed regenerates in 8–11 months after fission were examined (Fig. 3).

Table 2
Number of the orange stripes found in the orange-yellow-striped race.

No. of stripes	8	9	10	11	12	13	14	16	18	20
No. of regenerates	1	1	3	3	10	5	9	8	4	1
%	2.2	2.2	6.7	6.7	22.2	11.0	20.0	17.8	7.8	2.2

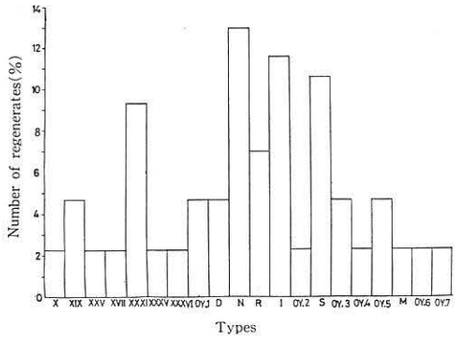


Fig. 3. Number of individuals belonging to various types produced by fission in the orange-yellow-striped race.

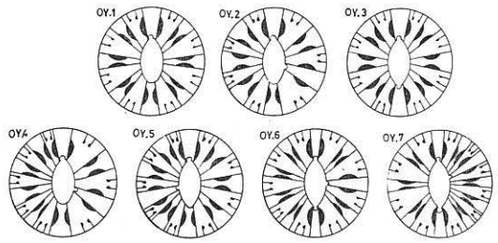


Fig. 4. Diagrammatic figures of peculiar types of the orange-yellow-striped race. OY. 1, mono-; OY. 2-OY. 5, di-; OY. 6 and OY. 7, tri-glyphics.

They comprised 13 mono-, 27 di- and 3 tri-glyphics belonging to various types. Many regenerates (76.4%), however, showed the same types as those in the orange-striped race already described (ATODA, 1972), while 7 types, OY.1–OY.7 (Fig. 4), were peculiar in this race. The number of the orange stripes varied with individuals (Table 2).

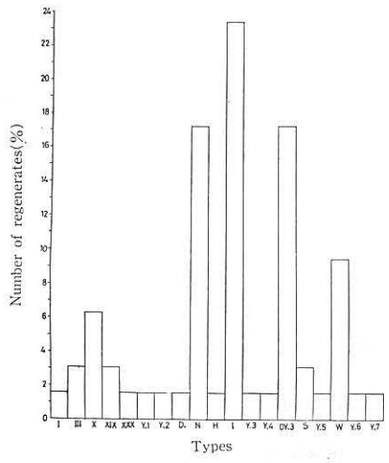
3. Yellow-striped race (YS) (Plate VII, Fig. 3)

The anemones had many yellow or whitish yellow stripes on their greenish columns. Most individuals collected from Tashiro Island had 48 stripes on the mesenteric chambers next the fourth order (Fig. 1C), whereas those obtained from Yunoshima had many deep yellow stripes on all chambers or every one chambers.

Forty-seven anemones collected from Yunoshima executed frequent fission and a considerable number of regenerates repeated fission at 20–26°C of sea water temperature during August to September. Usually two regenerates (89.1%), sometimes three (8.5%) and rarely four regnerates were produced from a single anemone by fission. Fission was performed in the same manner as found in two races mentioned above (Plate VIII, Figs. 7–11).

The types were observed in 64 regenerates in about six months after fission

Fig. 5. Number of individuals belonging to various types produced by fission in the yellow-striped race.



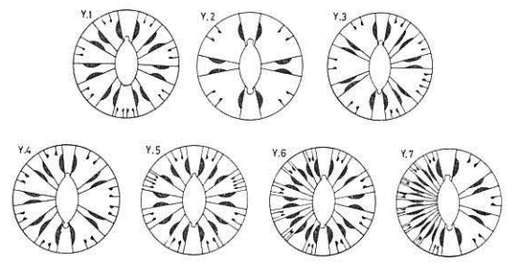


Fig. 6. Diagrammatic figures of peculiar types of the yellow-striped race. Y, 1, mono-; Y. 2-Y.7, di-glyphics.

(Fig. 5). Though 19 types were found, only a few individuals belonged to them except types I, N, W and OY. 3. Among them 11 types containing about 65% of regenerates were common to the orange-striped race, and one type, OY. 3 was common to the orange-yellow-striped race. Seven types, Y.1-Y.7 (Fig. 6), however, were peculiar in this race.

4. Non-striped race or NS (Plate VII, Fig. 4).

The anemones had no stripes on their columns and many thin streaks indicating attachment of mesenteries to body walls were seen (Fig. 1, D). The body assumed dark or greenish brown or brownish green. Fission occurred frequently at 20–27°C of sea water temperature during July to September.

The fissiparous process was almost similar to that of the orange-striped race and usually two regenerates were produced from a single parent by fission (Plate VIII, Figs. 1–6). Sometimes, however, some extra piece was separated from the body besides two portions and three regenerates arose (ATODA, 1960). The forms of 61 regenerates in about six months after fission were shown in Figs. 7, 8.

They comprised the mono-, di- and tri-glyphics as in the case of the other races

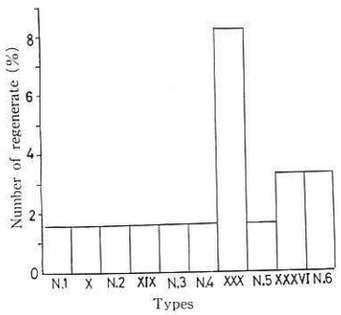


Fig. 7. Number of monoglycphics belonging to various types produced by fission in the non-striped race.

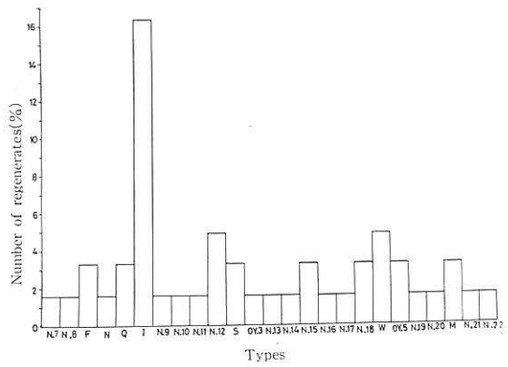


Fig. 8. Number of diglyphics belonging to various types produced by fission in the non-striped race.

and about 70% of them were diglyphic. About the half of regenerates belonged to the common types to those of the orange-striped race, while most of the remaining half belonged to 22 peculiar types (Fig. 9). It was very characteristic that such many peculiar types as well as much more various ones than the other races were found, while types N and XIX were few. The most individuals belonged to Type I, but they were only abot 16% of digilyphics.

5. Comparison of the forms between four races

The rate of the mono-, di- and tri-glyphics in the four races was shown in Table 3. The diglyphics predominated in all races, especially in the yellow-striped race. As to the types, the widest variations were found in the non-striped race, next orange-yellow-striped, then yellow-striped ones. On the contrary, the least variations were found in the orange-striped race collected from the fields (ATODA, 1972) (Table 4).

As it was noticed from Figs. 3, 5, 7 and 8, there were a considerable number of common types to the three races except the non-striped one in which such types were rather few. On the contrary, the number of the peculiar types were the reverse to that of the common ones (Table 5).

On the other hand, among 105 types obtained from all races, only 5, X, XIX, I, N. S were common to all, and Type I in mentioned three races, and N in both the orange-yellow-striped race and yellow-striped one appeared in a considerable number. Besides such types, only a few were common to these three races and also to two races, orange-yellow-striped and yellow-striped or non-striped.

In regard to the mesenteries (Fig. 10) the individuals with six pairs of principal mesenteries, viz., two pairs of the directives and four pairs of the

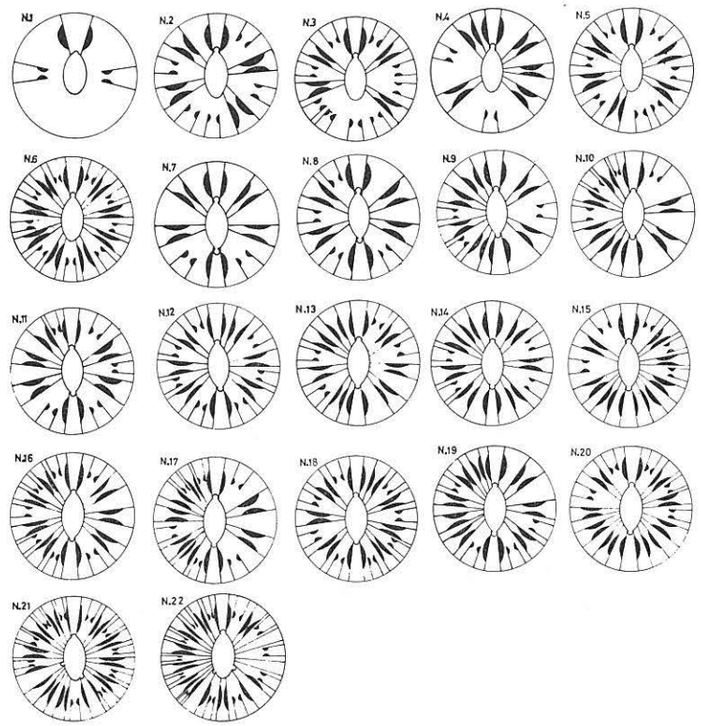


Fig. 9. Diagrammatic figures of peculiar types produced by fission in the non-striped race. N.1-N.6, mono-; N.7-N.20, di-; N.21 and N.22, tri-glyphics.

Table 3

Respective rate of the mono-, di- and tri-glyphics in the four races (%).

Races	No. of individuals	Monoglyphics	Diglyphics	Triglyphics
OS produced by fission	20	20.0	70.0	10.0
OS collected from fields	293	33.1	60.4	6.1
OY	43	30.2	62.8	7.0
YS	73	15.1	84.9	0
NS	61	26.2	67.2	6.6

first order, remarkably predominated in the orange-striped race, while none of such dominant ones were found in the other races. In both the orange-yellow-striped race and the yellow-striped one seven pairs of such mesenteries and in the non-striped race nine, next seven pairs somewhat predominated. As to the number and arrangement of these mesenteries, the orange-striped race showed a fairly different tendency from the others, and the orange-yellow-striped race was rather similar to the yellow-striped one, while in the non-striped race the characteristic tendency was recognized.

Table 4
Respective variations of the types in the four races.

Races	All individuals		Diglyphics	
	No. of types	Rate of variation (%)	No. of types	Rate of variation (%)
OS produced by fission	13	65.0	7	50.0
OS collected from fields	34	11.6	13	7.3
OY	20	46.5	9	33.3
YS	19	26.0	13	24.5
NS	32	52.5	22	53.7

Table 5
Common types of the three races to the orange-striped race, and their peculiar types.

Races	Common types (%)	Peculair types (%)
OY	60.0	25.0
YS	57.9	36.8
NS	34.4	62.5

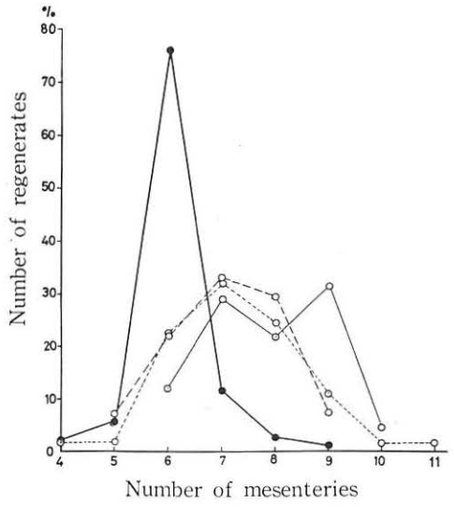


Fig. 10. Number of principal mesenteries (pair) of four races. Thick, thin, dotted and brocken lines indicate the orange-, non-, yellow- and orange-yellow-striped races respectively.

B. Pedal laceration in the orange-striped race

1. Regenerates developed from the pieces, I-II-D

This piece consisted mainly of stumps of the directive, first and second orders of mesenteric chambers (Fig. 11, B).

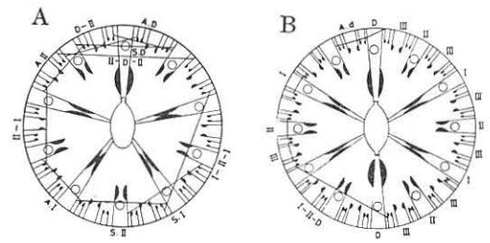


Fig. 11. Various kinds of pieces made in the previous experiments (A) and in the present ones (B)

Table 6
Types of regenerates developed from two kinds of pieces, I-II-D and A.d.

Pieces	I-II-D					A.d			
Types	A	D	F	N	I	XVI	XIX	N	S
No. of regenerates	2	6	3	7	2	1	1	7	1

In about seven weeks after regeneration, the forms of 20 well-developed regenerates were examined and following results were obtained (Table 6).

All regenerates were diglyphic belonging to five types found in the individuals collected from the fields (ATODA, 1972) and produced by artificial laceration (ATODA 1960).

2. Regenerates developed from the pieces, A. d

This piece (Fig. 11, B) was closely similar to the piece, A. D (Fig. 11, A), but had a smaller directive chamber than it.

Ten regenerates with 10 to 14 deep orange stripes in about three months after regeneration comprised 2 mono- and 8 di-glyphics (Table 6). As the triglyphics originated from A. D pieces (ATODA, 1960), it was expected that such individuals may appear from this pieces. The monoglyphics seemed to originate from the pieces with only one moiety of a pair of the directives.

3. Regenerates developed from long pieces

The anemones used to make pieces were of smaller size, having pedal discs measuring about 7 mm in diameter. The discs were cut along their peripheries and the pieces thus made had at least 7 orange stripes and two pairs of directives. Such a long piece, however, was never produced by natural laceration.

In about 3 months after regeneration 29 well-developed individuals with 7 to 14 deep orange stripes were obtained, of which 12 were triglyphic (Plate IX, Figs. 1–6) as expected. In addition to them 15 diglyphics belonging to the types, F, I, N, V. Q and L.1–L.4 (Fig. 12) and two tetraglyphics (Plate IX, Fig. 7) were observed. The forms of all tri- and tetra-glyphics and four types of diglyphics,

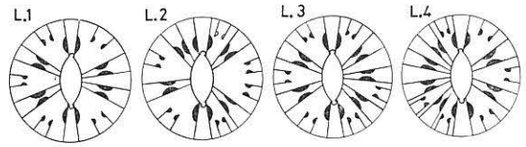


Fig. 12. Diagrammatic figures of peculiar types found in the diglyphics arising from the long pieces.

Table 7
Types of 26 regenerates developed from small pieces.

Mesenteric chamber of pieces	I		II				III					
Types	XIX	X	XII	XIX	N	X	III	XIX	XXIV	N	Q	M
No. of regenerates	1	2	1	1	1	1	4	7	1	5	1	1

L.1–L.4, were peculiar and characteristic. Besides them a single diglyphic regenerate had two oral apertures (PLATE IX, Fig. 8).

4. Regenerates developed from small pieces

The pieces having about 1 mm square in size, consisting of only a single mesenteric chamber, viz., the first, second or thrid order, and none of the directives were contained (Fig. 11, B). Twenty-six regenerates developed well in about four months after regeneration and following results were obtained (Table 7).

It has been reported that the diglyphics originated from the pieces with the directives and the monoglyphics from those without them (ATODA, 1960). In this experiment, however, a considerable number of the diglyphics (26.9%) belonging to the types, N and Q, arose from such pieces as I, II and III. Moreover the triglyphics, M and X originated from them.

5. Processes of regeneration

In the present experiments and previous ones (ATODA, 1960) all kinds of pieces (Figs. 11A, B) were rolled inside and fused together in their bilateral free edges as described by HAZEN (1902, 1903) and CARY (1911). Consequently they became conical in shape with whitish streaks indicating fused portions in a few days. At first several tentacles appeared as small swellings at tips of the regenerates within about five days after regeneration, and were quickly elongated (Figs. 13, A, B). The oral apertures were formed somewhat later than an appearance of tentacles, then stomodeums were differentiated.

The oral aperture was open at a tip of stumps of directives in all pieces with the directive systems (Plate VIII, Figs. 15, 16), and these stumps soon became the directives of the regnerate. Another pair of directives were formed on the oposite side of the old ones, and several new mesenteries appeared successively on

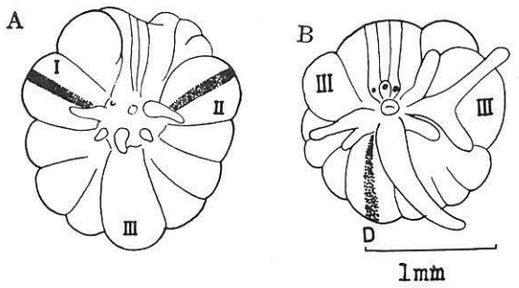


Fig. 13. Development of tentacles in regenerates arising from the piece I-II in 5 days (A) and from the piece S. D in 11 days (B) after regeneration.

either side of new directives. As the tissues of the oral aperture and stomodeum to which the directives attached differentiated to the siphonoglyph, the diglyphics originated from the picees with a pair of directives.

The regenerates which have mesenteries arranged regularly in the bilateral symmetry as found in type N were apt to originate from such pieces as S. D and 11-D-11 which included the directives to their middle parts (Fig. 11, A). On the other hand, asymmetrical arrangement of mesenteries were often observed in the regenerates developed from such pieces as D-11 and I-II-D, then A. D and A. d, which included the directives in either end of the pieces.

In the pieces which have the first order of chambers in stead of the directive ones, viz., S.I, A.I and I-II (Fig. 11, A), the oral aperture appeared at the tip of stumps of the first order of mesenteries (Plate VIII, Figs. 12, 13), and this stumps became the same order of mesenteries of the regenerate, and a new pair of directives were formed on the opposit side of mentioned mesenteries (Plate VIII, Fig. 13). In the piece, I-II-I, which had two first order of mesenteries, the oral aperture appeared at the tip of stumps of mesenteries just described and new directives developed between them in the regenerative part. On the contrary, in the pieces without both directives and the first order of mesenteries, viz., S. II, A. II and III-IV (ATODA, 1954b), the oral aperture was open at a tip of the piece regardless of the mesenteries (Plate VIII, Fig. 14). In all kinds of pieces without directives, only a single pair of new directives were regenerated, and thus the monoglyphics originated from them.

On the other hand, regenerative processes of such small pieces as I, II and III and those of long ones with two pairs of directives differed from the others. In the former two or three pairs of directives were formed in regenerative portions of some regenerates and in the latter no directives or one or two pairs of directives were regenerated, and thus the di-, tri- or tetra-glyphic individuals originated from these pieces.

CONSIDERATION

Although the orange-striped race usually reproduced by pedal laceration,

several individuals executed fission as reported by DAVIS (1919), MIYAWAKI (1952) and UCHIDA (1936). In the remaining races their asexual methods of reproduction were fission and never laceration. It was considered from this point that fission was the original method of asexual reproduction in the present species and perhaps laceration was induced secondary from fission.

Usually two portions having a single pair of directives and one siphonoglyph respectively were produced by fission and the diglyphics originated from them. Such a mode of fission was regarded as a normal form. Therefore, though a good number of monoglyphics were observed in all races, the diglyphics were regarded as the typical forms of these races and monoglyphics were abnormal ones.

The various types occurred in these races and the least variations were found in the orange-striped one collected from fields. Moreover type N alone remarkably predominated in this race, while such a dominant types did not appear in the remaining races. Accordingly this race should be regarded as the most stable one and type N as the original form in this race. Each of the types of the other races appeared at considerably lower rate and it was difficult to determine their original types.

Such various forms, however, are attributed to fission as recognized in the individuals of the orange-striped race produced by fission, and it may be not adequate to investigate their relationships from their forms. Nevertheless it seems that the orange-striped race is rather distantly related to the remaining races and the orange-yellow-striped race and yellow striped one are a nearer relation, while the non-striped one is further distantly related to them.

On the other hand, as to laceration in the orange-striped race, regenerates had an inclination to form a single pair of directives in their regenerative parts. Accordingly the di- or mono-glyphics originated from respective pieces with or without directives (ATODA, 1960). Nevertheless the diglyphics appeared from very small pieces without directives. Almost whole portions of body were newly formed in these pieces, and it was considered that complete regeneration was performed and consequently the original form stated above appeared. On the contrary, a good many regenerates which arose from the long pieces minimally regenerated and none of directives were formed in their regnerative portions.

Usually many small pieces without stripes were observed in laceration (ATODA 1973) and the diglyphics may arise from them besides the pieces with directives. In addition to them type N must be produced by sexual reproduction, and thus the diglyphics, especially type N may predominate in this race.

SUMMARY

1. A small number of individuals belonging to the orange-striped race executed fission and regenerates with various forms originated.

2. All of the remaining races also executed fission in a similar manner and never acted pedal laceration.

3. The wide variations occured in their types and none of the dominant ones were observed in regenerates of three races except the orange-striped one.

4. In the orange-striped race the diglyphics originated from all kinds of the pieces with directives, I-II-D, A. d and the others and in addition to them from the small pieces without directives, viz. I, II and III. The triglyphics originated too from such small pieces.

5. The di-, tri- and tetra-glyphics originated from the long pieces with two directive chambers. Such pieces, however, never appeared in natural pedal laceration.

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Explanation of Plate VII-IX

Plate VII

Figs. 1–4. Four races, orange-striped (1), orange-yellow-striped (2), yellow-striped (3) and non-striped (4). × 1.3

Figs. 5–11. Processes of longitudinal fission in the orange-striped race. Beginning of fission (5) and 5 min later (6). Body begun to tear in 27 min (7), then 32 min (8), 1 hr 5 min (9) and 2h 35 min later (10). Body split into two in 18 hr (11).

Figs. 12–15. Processes of longitudinal fission in the orange-yellow-striped race. Beginning of fission (12). Body begun to tear in 2 hr 5 min (13) and almost split into two in 2 hr 25 min (14). Fission finished in 3 hr 25 min (15).

Figs. 16–19. Another fission in the race described above. Rent begun to appear at a center of the oral disc (16) and it widened in 45 min (17). Body begun to split into three in 3 hr 45 min (18) and three regenerates originated in 22 hr 45 min (19).

Plate VIII

Figs. 1–6. Processes of longitudinal fission in the non-striped race. Beginning of fission (1) and 45 min (2), then 1 hr later (3). Body begun to tear in 1 hr 35 min (4) and split into two in 1 hr 51 min (5). Two regenerates originated in 20 hr (6).

Figs. 7–11. Processes of longitudinal fission in the yellow-striped race. Early process of fission (7), then 37 min later (8). Body begun to tear in 3 hr 47 min (9) and almost split into two in 23 hr 10 min (10). Two regenerates originated in about 36 hr (11). × 2

Fig. 12. Individual developed from the piece S. I in 14 days after regeneration. I, the first order of mesenteries. × 33

Fig. 13. Individual developed from the piece I-II in 9 days after regeneration. Oral aperture was open at a tip of the first order of old mesenteries (I) as found in Fig. 12. New directives (D) already developed. × 28

Fig. 14. Individual developed from the piece A. II in 10 days after regeneration. Oral aperture was open apert from the second order of old mesenteries (II). ×42

Fig. 15. Individual developed from the piece I-II-D in 44 days after regeneration. Oral aperture was open at tips of both old directives (D) and the first order of old mesenteries (I). × 23

Fig. 16. Individual developed from the piece II-D-II in 23 days after regeneration. Oral aperture was open at a tip of old directives (D). × 25

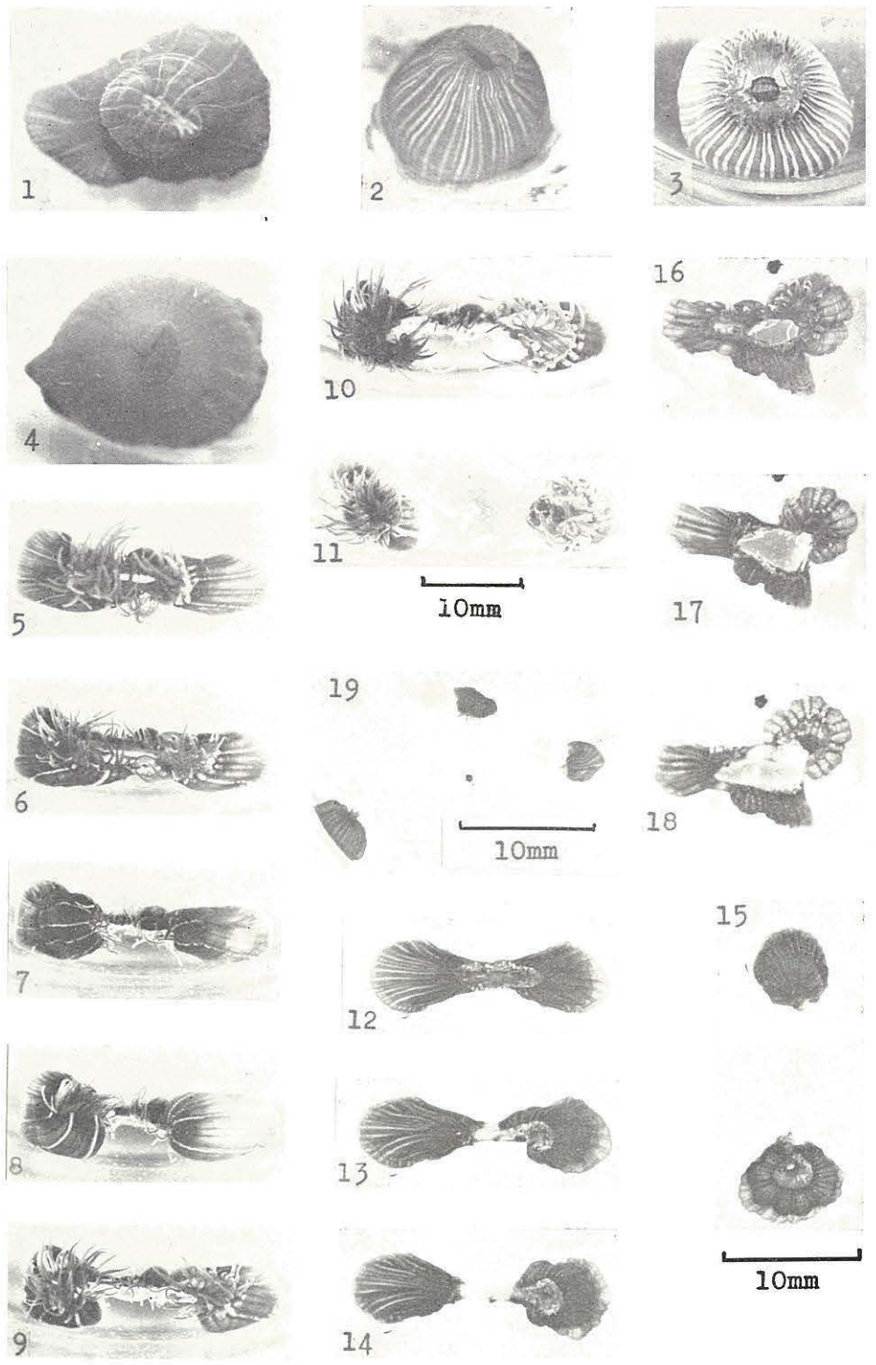
Plate IX

Various types of individuals developed from the long pieces in about three months after regeneration. D, directives.

Figs. 1–6. Triglyphic individuals. × 30

Fig. 7. Tetraglyphic individual. × 20

Fig. 8. Individual with two oral apertures. × 20



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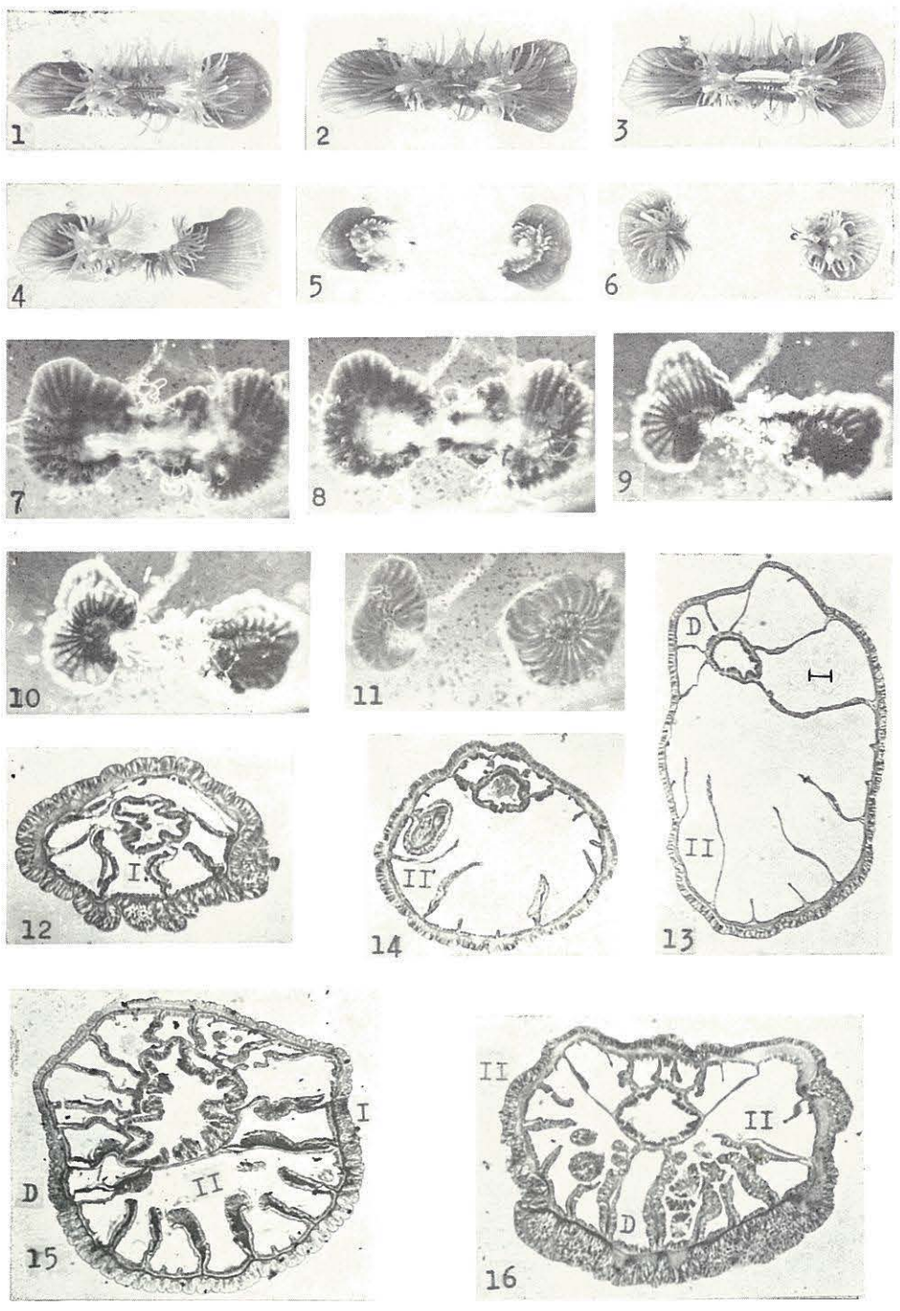
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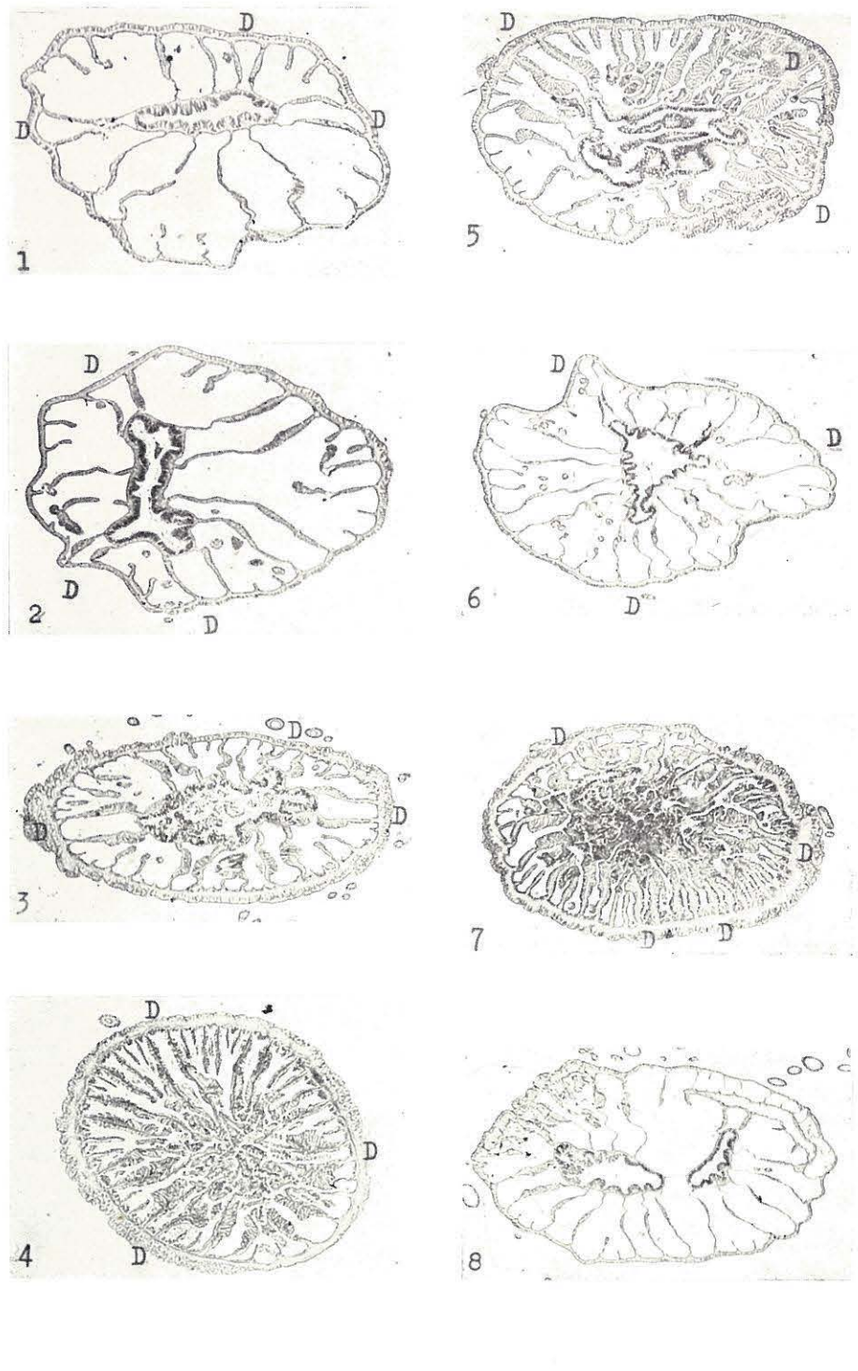
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